BIOSTRATIGRAPHIC IMPLICATIONS OF FOSSIL KANGAROOS AT RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Kangaroos form an important component of the faunal assemblages of Riversleigh and most other Australian Cainozoic fossil deposits. Attempts to use fossil kangaroos to determine the relative ages of Riversleigh sites suggests that overall faunal composition may be a more useful guide to relative age than presence or absence of particular species. Marked changes in kangaroo faunal composition occur between Riversleigh System B and C sites with the apparent extinction of most balbarine species and rise to dominance by lophodont bulungamayine species. This change correlates with climatic decline following mid-Miocene climatic optima. Approximate age equivalence is suggested between Riversleigh System B sites and faunal zones B + C (Woodburne et al., 1993) of the Etadunna Formation, South Australia. Riversleigh's System A sites are older. The more derived, lophodont bulungamayines of Riversleigh System C are considered potentially ancestral to plesiomorphic macropodids such as *Hadronomas* from the Alcoota Formation. Kangaroos support an age span for pre-Pliocene deposits at Riversleigh that extend from the late Oligocene to late middle Miocene and possibly early late Miocene. □ *Kangaroos, Oligocene, Miocene, Pliocene, Riversleigh.*

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Tedford (1967) provided the first description of kangaroos from Riversleigh. Since then the area has yielded many thousands of kangaroo fossils representing at least 32 new species.

Archer (1979) described *Wabularoo naughtoni* from D Site. Flannery et al. (1982) described *Bulungamaya delicata* (erecting the Bulungamayinae), *W. naughtoni*, *Balbaroo gregoriensis* from Riversleigh. *B. camfieldensis* from Bullock Creek, Northern Territory (middle to Late Miocene) and a single specimen of *Balbaroo* from Kangaroo Well. The species of *Balbaroo* were placed in a new macropodid Balbarinae. They also described the potoroine *Gumardee pascuali* and macropodid *Galanarla tessellata* from Riversleigh.

Archer & Flannery (1985) described the Riversleigh propleopine *Ekaltadeta ima*. Flannery & Archer (1987a) described *Hypsiprymnodon bartholomaii* and (1987b) *Bettongia moyesii*, the only pre-Pliocene representatives of these genera. Cooke (1992) described the balbarine *Ganawamaya* with *G. acris*, *G. aediculus* and *G. ornata*.

The number of Riversleigh fossil kangaroo specimens, ranging from isolated teeth, isolated postcranial elements, maxillary and dentary fragments to complete skulls is almost overwhelming. I have concentrated on the more complete

remains available. These indicate a further 21 new species, a number of which are described in this volume. *Protemnodon* sp. has been recorded from the Pliocene Rackham's Roost Site and *Macropus agilis* has been recorded from the Pleistocene Terrace Site (M. Archer pers. com.).

This brings the total Riversleigh macropodoid fauna to 34, including the Potoroinae, Hypsiprymnodontinae, Propleopinae, Balbarinae, Bulungamayinae and Macropodinae.

Archer et al. (1989) recognised more than 100 local faunas from the Riversleigh fossil area, with ages estimated to range from Oligocene-Miocene to Holocene. (Discoveries since 1989 have raised that number to more than 150 sites with faunal assemblages). They grouped the Oligocene-Miocene sites into three 'Systems' designated A-C, with System A sites regarded as oldest and System C sites as youngest.

Megirian (1992) treated the entire sequence of fossiliferous Limestone overlying the Thorntonia Limestone as comprising the Carl Creek Limestone. He used the 'Systems' of Archer et al. (1989) in a purely biostratigraphic sense and has later (1994) challenged the use of the System concept on the grounds that the terminology has been unsatisfactorily defined and that there is no precedent for such usage in lithostratigraphic nomenclature.

TABLE 1. Sites of occurrence and numbers of specimens of each identified pre-Pliocene Riversleigh macropodoid species.   QL=Quantum Leap; WH=White Hunter; DU=Dunsinane; COA=Cleft of Ages; BA=Bitesantennary; DT=Dirk's Towers; OUT=Outasite; WW=Wayne's Wok; BO=Boid; CS=Camel Sputum; IN=Inabeyance; MM=Mike's Menagerie; UP=Upper; CR=Creaser's Ramparts; N'sG=Neville's Garden; LM=Last Minute; FF=Fireside Favourites; H'sH=Henk's Hollow; TT=Two Trees; DO=Dome; J'sC=Jim's Carousel; ENC=Encore; ?=uncertain position within the System sequence of Archer et al. (1989).

SPECIES	Syst. A D	Syst. A G	?A/B QL	?A/B WH	?A/B DU	?A/B COA	?A/B BA	?A/B DT	Syst. B Lower RSO	Syst. B Lower OUT	Syst. B Lower WW	Syst. B Higher BO	Syst. B Higher CS	Syst. B Higher IN	Syst. B Higher MM	Syst. B Higher UP	Syst. B Higher CR	?B Intr. N'sG	Syst. C Low C GAG	Syst. C Low C LM	Syst. C Mid C low	Syst. C Mid C High-er	Syst. C Higher C FF	Syst. C Higher C H'sH	Syst. C Higher C TT	Syst. C ?	?mid Mio DO	?mid Mio J'sC	Uncert. ENC
gen.Wan. sp.1																			2								1		1
gen.Wan. sp.2																				1				3					1
Bu.dalicata	1	1	3					1	2		11	16				9		1	3										
Wab. naughtoni	1	1		6					1		23	19		2	6			5											
Gan. bilamina							1				7	4		1	4														
Gan. sp.2																			3	1				3				2	
Bat. moyesii																			1						1				
E. ima																			1										
H. bartholomaii																			1										
Gum. pascuali	1																												
Now. matrix				1								4	7			1													
Now. sp.2			2																										
Bal. gregoriansis		1						1				3	1	1	1		2	1											
Bal. sp.2										1																			
Bal. sp.3				1																									
Bal. sp.4																							1	2					
Gal. tassellata	5	1																											
Gan. acris									1				1																
Gan. aediculis				1																									
Gan. ornata												1																	
Gan. sp.4																	1												
Wur. dayamayi				1																									
Wur. sp.2						1			2			4		2															
Wur. sp.3													1																
Nam. couperi				1																									
Nam. sp.2												2																	
Nam. sp.3			1									1																	
Nam. sp.4												1																	
Nam. sp.5				1				5				1	1			1		2											
Nam. sp.6												1	2					1											
Nam. sp.7													1																
Nam. sp.8			1																										

Archer et al. (1989) Archer, Hand and Godthelp (1991) and Archer et al. (1994) interpreted the older Riversleigh local faunas, those from sites in Systems A-C, as representing rainforest communities. This interpretation was made on the basis of characteristics of those faunas such as: high species diversity; presence of complex feeding guilds of small, sympatric mammals; high numbers of obligate leaf eaters in single local faunas, indicating high tree species diversity; presence of high numbers of known rainforest taxa; high numbers of browsing marsupials but absence of grazers.

Megirian (1992) disputed the hypothesis of a rainforest palaeohabitat for the older Riversleigh local faunas on the grounds of his interpretations of drier, even semi-arid environmental conditions prevailing during the genesis of the fossiliferous limestones. He suggested instead that the high species diversity evident in the local faunas resulted from a combination of resident rainforest communities inhabiting rainforest refugia confined to permanent water bodies, and the use of such permanent water by animals drawn from more distant, mesically adapted communities.

None of the Pre-Pliocene kangaroos from Riversleigh exhibit dental adaptation for a grazing habit which might be expected if they were drawn from a more arid environment. Regardless of their palaeohabitat, kangaroos have a widespread occurrence and are abundant among the many local faunas now known from Riversleigh. They should prove to be important in attempts to determine relative ages of those assemblages. This paper presents the results of a preliminary attempt to use kangaroo fossils to assess relative ages of sites within Riversleigh, assess the age of Riversleigh deposits relative to those of other Australian Tertiary sites which have yielded comparable kangaroo fossils, and to correlate changes apparent within the macropodoid fauna of Riversleigh with Tertiary climatic and geologic events. As part of that attempt, the Systems concept of Archer et al. (1989) has been used as an hypothesis which can be tested using the dis-

tribution of fossil kangaroo species in sites previously assigned to each of systems A, B and C.

INTER-SYSTEM COMPARISONS AND OTHER RELATIONSHIPS AT RIVERSLEIGH

Pre-Pliocene Riversleigh sites that have yielded identified macropodoid species, together with the number of specimens of each, are shown in Table 1.

Column headings in this Table follow Archer et al. (1994) who listed sites known to that date, indicating those confidently assigned to Systems A-C, provided indications of possible System affinities of some sites, and estimated ages of other sites whose faunal composition differs from those allocated to these Systems. As indicated in Table 1 and discussed further below, evidence drawn from the distribution of kangaroo fossils is not in complete agreement with ages suggested by Archer et al. (1994) for some Riversleigh sites. Site G of Flannery et al. (1982) is included within System A on this table since it is described by those authors as lying within the Carl Creek Limestone.

Late Oligocene (Archer et al., 1995; Myers & Archer, this volume) System A may have been a time of 'icehouse conditions' with relatively low temperature, rainfall and biodiversity (Frakes et al., 1987).

Five macropodoid species have now been identified in System A sites. Of these, *Balbaroo gregoriensis* and *Wabularoo naughtoni* are known also from System B and *Bulungamaya delicata* occurs in sites in all 3 Systems. *Gumardee pascuali* and *Galanarla tessellata* are so far known only from System A. Unfortunately molar teeth preserved in the holotypes of the last two species are badly worn and/or damaged, reducing their usefulness for biostatigraphic analysis. However, lower molars of *Galanarla tessellata* exhibit a well-developed posterior cingulid linked to a postentocristid, a feature typical of balbarines (see Cooke this volume), but not present among bulungamayines.

G. tessellata is here assigned to the Balbarinae. As noted by Flannery et al. (1982), *Gumardee pascuali* is of comparable size to *Wabularoo naughtoni*, a common variable species within Riversleigh's Systems A and B. *G. pascuali* is considered to fall within the range of variation observed among specimens of *W. naughtoni*.

Nambaroo, Wururoo (Cooke, this volume) and *Ganawamaya, Balbaroo* sp.2, *Nowidgee matrix* (Cooke, this volume) and *Ganguroo bilamina*

(Cooke, this volume) all occur in System B, but not in System A or C. These taxa in newly discovered sites of unknown relative age may therefore be suggestive of an age comparable to other System B sites. Occurrence of *B. delicata in* all three systems and of *W. naughtoni* and *B. gregoriensis* in Systems A and B suggests that caution is indicated before declaring any of the above taxa, so far found only in System B, as definitive indicators of that System. *Balbaroo gregoriensis*, for instance, is more derived in molar morphology than any *Nambaroo* and it seems likely that representatives of the latter plesiomorphic balbarine and perhaps of others, such as *Wururoo* and *Ganawamaya*, may also ultimately he found in System A. If System B sites are correctly interpreted as early Miocene in age (Archer et al., 1994, 1995), remains found in those sites may have accumulated during 'greenhouse conditions' with high temperatures, rainfall and biodiversity (Frakes et al., 1987).

The macropodoid fauna of System C is more distinctive than those of Systems A and B, containing representatives of 5 subfamilies: 4 species of Bulungamayinae and 1 each of Hypsiprymnodontinae, Potoroinae, Propleopinae and Balbarinae. Of the 8 macropodoid species known from System C, *Bulungamaya delicata* is the only one occuring in other Systems. Of the remainder, *Wan* (which includes the 'Gag Site macropodine' of Flannery, 1989) and *Ganguroo* sp.2 are among the most highly derived bulungamayines and *Balbaroo* sp.4 is more derived in molar morphology than any other known balbarine species. Presence of these species in particular in any given site may suggest but not define an age comparable to, or perhaps younger than that of System C sites. Archer et al. (1994, 1995) suggested that System C is middle Miocene. If this is so, this interval was also characterised by 'greenhouse conditions' (Frakes et al., 1987).

Overall macropodid faunal composition, rather than presence of particular species, may provide a more reliable guide in assessing relative ages of Riversleigh sites. If *Galanarla tessellata* is accepted as a balbarine and *Gumardee pascuali* as a bulungamayine, these subfamilies are represented in System A by 5 species, roughly equally divided among between the two: 3 bulungamayines versus 2 balbarines, with 7 identified specimens from each subfamily. System A deposits may thus be characterised by roughly equal diversity and abundance of balbarine and bulungamayine species.

The diversity of macropodoid species is greatest in absolute terms in System B. Balbarines and bulungamayines are both present, with balbarines dominating in terms of numbers of species (13 versus 4). If numbers of identified specimens are taken as a crude guide to abundance within species, bulungamayines appear to have been more abundant, the 3 species of lophodont bulungamayines being represented by a total of 102 specimens, compared to a total of 32 balbarine specimens from 12 species. System B deposits may thus be characterised by high species diversity of balbarines with accompanying low species abundance, and by a lower species diversity of bulungamayines but a relatively higher abundance of members of those species.

Subfamilial diversity is greatest in System C, but Potoroinae, Hypsiprymnodontinae and Propleopinae are each represented by single species. Among the lophodont species, bulungamayines have gained the ascendancy over balbarines in terms of numbers of species (4 versus 1) and in relative abundance (16 identified specimens versus 3).

System C may thus be characterised by dominance of lophodont bulungamayines, low incidence of balbarines and possible hypsiprymnodontines, propleopines and potoroines, although undescribed propleopine remains are known from sites such as Dirk's Towers which is probably equivalent in age to system B.

Lower absolute diversity in System A deposits may result from cooler, drier climatic conditions, exacerbated by the lower number of System A sites (2) yielding identified macropodoid species, compared to the number of System B sites (10) yielding such species. Macropodoid diversity within System A is thus likely to have been higher than that currently known.

System B deposits are suggested to have accumulated in pools or shallow lakes and System C deposits in deep pools, shallow pools or emergent accreting surfaces, or cave outwashes (Archer et al., 1994). Depositional environments are thus more comparable for Systems B and C. The probabilities of accumulating remains of terrestrial mammals are also likely to be comparable for these systems. Differences in overall macropodoid faunal composition between these two Systems are therefore more likely to be a true reflection of conditions prevailing during the times of deposition of these Systems.

There is a striking change in macropodoid faunal composition between Systems B and C. With the exception of a single, highly-derived lopho-

dont, Balbaroo sp.4, browsing balbarines are apparently absent from System C, as is Wabularoo naughtoni which persists through Systems A and B. Bulungamaya delicata persists only in sites low in the sequence of System C deposits. System B omnivores, such as Nowidgee, are replaced in System C by Bettongia moyesii and Hypsiprymnodon bartholomaii. Compared to System B, System C macropodoid assemblages are depauperate in numbers of species and dominated by larger, derived, lophodont bulungamayines whose long premolars and general molar morphology bear strong similarities to those of plesiomorphic macropodids. The System B macropodoid assemblages have a high species diversity, particularly among balbarines. High faunal diversity is a characteristic of rainforest habitats, suggested by Archer et al. (1989) to be the habitat for older Riversleigh local faunas (including those from System C). The decline in overall macropodoid diversity evident within System C and the dominance of larger, lophodont bulungamayine species suggests that rainforest habitat indicated by Archer et al. (1989) may have been in decline during accumulation of System C. That this was not a sudden event is indicated by the persistence of the presumably rainforest adapted B. delicata into the lower levels of System C at Gag Site, the occurrence at this same site of Hypsiprymnodon, modern representatives of which are confined to rainforest in northern Queensland, and the occurrence there of a high diversity of possum species (Archer et al., 1991).

Archer et al. (1994, 1995) estimated the age of System B as early Miocene and System C as middle Miocene. McGowran & Li (1994) correlate the planktonic foraminifera record of southern Australia, oceanic d^{18}O levels and sea level fluctuations and indicate generally warmer, wetter climatic conditions during the Oligocene-early Miocene, with 3 warm and moist climatic optima occurring during the Miocene. Two of these occur during the early Miocene during the Janjukian and Longfordian stages respectively, and a double-peaked optimum occurred during the early middle Miocene, corresponding with Batesfordian and Balcombian stages, 16-15ma. Following the latest of these climatic optima there is a general and world wide decline towards a cooler, drier climatic regime associated with a 'reverse greenhouse' effect. In northern Australia the effects of this decline would have been exacerbated by the middle Miocene uplift of the New Guinea Highlands. Archer et al. (1989) have sug-

gested these newly upthrust mountains could have created a 'rain shadow' effect across northern Australia which may have been one of the most important factors causing the decline of central and northern Australian rainforests. The climatic decline following the early middle Miocene climatic optimum coincides well with the early middle Miocene estimate of Archer et al. (1994, 1995) for the System B/C boundary. It is therefore likely that the decline in macropodoid diversity at the System B/C boundary is a reflection of the combined effects of the geological and climatic phenomena outlined above.

A number of Riversleigh sites are of uncertain stratigraphic relationship. The local biostratigraphic implications of the macropodoid taxa which have been found in some of these are discussed below.

The low stratigraphic position of White Hunter Site and its unusual faunal assemblage make it uncertain whether it belongs to System A or B. Of its 7 identified macropodid taxa found, 5 are unique to the site and, of themselves, do little to settle the question either way. Of the remainder, the plesiomorphic balbarine, *Nambaroo* sp.8, is found elsewhere only at Dunsinane Site whose relative age is also uncertain (but see Arena, this volume). *Nowidgee matrix*, is found only within System B at sites in both lower and higher levels of the sequence. The occurrence of this species and the overall composition of the macropodoid fauna of White Hunter Site — dominated by plesiomorphic balbarines with 2 plesiomorphic bulungamayines, suggests that the site is possibly a basal member of the System B sequence. The 2 species of *Nambaroo* found in this site are extremely plesiomorphic balbarines (Cooke, this volume) and the species of *Nowidgee* found there are similarly plesiomorphic bulungamayines (Cooke, this volume). Occurrence of such plesiomorphic species in the one site sugests that White Hunter may be even older, perhaps belonging to System A (Creaser, this volume). The latter interpretation is supported by Myers & Archer (this volume) who report the occurrence at White Hunter Site of *Kuterintja ngama*, an ilariid conspecific with one in the Mammalon Hill Local Fauna of central Australia that is dated as 24myo (late Oligocene) by magnetostratigraphy.

The occurrence of *N*. sp.8 at Dunsinane Site complicates rather than clarifies understanding of this already enigmatic site in which are preserved plant material, insects and fossil bone. Dunsinane occurs in an area close to the boundary of the Tertiary limestone and Precambrian quartzite.

The occurrence of this plesiomorphic balbarine suggests the site may be equivalent in age to White Hunter Site, but there are several reasons for caution. No other vertebrate remains supporting this age determination have so far been identified from this site. All vertebrate remains here are fragmented and poorly preserved and may well have been re-deposited after previous reworking.

Bitesantennary Site and Dirk's Towers Site are both intrusive deposits on the D Site Plateau, regarded as probably equivalent to System B assemblages (Archer et al., 1994). Only a single macropodoid, *Ganguroo bilamina*, has been identified from Bitesantennary Site, but this species is otherwise known only from System B. Dirk's Towers Site has 3 macropodoids, including *Bulungamaya delicata*, known from Systems A, B and C. *Balbaroo gregoriensis* is known from both Systems A and B. However, *Nambaroo* sp.5, is known only from System B. On balance, macropodoid fauna of Dirk's Towers Site supports a System B age.

Archer et al. (1994) suggested that the faunal assemblage of Quantum Leap warrants its likely inclusion in System A. Only 3 macropodoid species are so far known from this site. *Bulungamaya delicata* is uninformative since it occurs in all 3 Systems. However, 2 species of *Nambaroo* are known from the site, both species otherwise known from System B sites or those likely to be of equivalent age, e.g., Dirk's Towers and Neville's Garden Sites. The macropodoid fauna of this site therefore suggests a closer affinity with System B rather than System A.

Neville's Garden Site is a possible cave outwash deposit considered to be equivalent in age to System B (Archer et al., 1994). Macropodoids of this site include the ubiquitous *B. delicata*, *W. naughtoni* and *Balbaroo gregoriensis*, the latter two occurring in systems A and B, and 2 species of *Nambaroo* known from both upper and lower levels of System B. The occurrence of the latter species and the typical System B composition of the Neville's Garden macropodoid fauna support a System B age for this site.

Dome Site, Jim's Carousel Site and Cleft of Ages Site have all been suggested to be younger than System C sites (Archer et al., 1994). Gen.*Wau*. sp.1 (the 'Gag Site macropodine') is the only macropodoid so far identified from Dome Site. It is known elsewhere only from Gag Site in System C and Encore Site of possible late Miocene age (Archer et al.,1994). *Ganguroo* sp.2 is the only macropodoid so far known from Jim's

Carousel Site. This species is also known from Gag and last Minute Sites, low in the sequence of System C deposits, and from Henk's Hollow Site in the higher levels of that sequence.

Both species are highly derived bulunga-mayines which first appear in System C, but there is no reason to suggest that they may not have persisted beyond System C. Their presence in Dome and Jim's Carousel Sites therefore cannot confirm or deny the younger age postulated for these sites.

The single macropodoid, *Wururoo* sp.2, from Cleft of Ages is a plesiomorphic balbarine otherwise known only from System B. Its presence therefore suggests system B. This is in conflict with wombat teeth in this site, not known from any of the older Riversleigh sites, and the 'generally more modern' (presumably 'more derived') appearance of other remains (Archer et al., 1989).

Encore Site has been suggested to be younger still, possibly late Miocene (Archer et al., 1994). Encore has 2 highly derived bulungamayine species, gen. *Wan.*, spp. 1&2. Both species are known from System C, but there is no reason to suggest that these moderately robust, lophodont species might not persist beyond the age of that system. Their presence does not preclude the age estimated for this site.

MACROPODOID CORRELATES BETWEEN RIVERSLEIGH AND OTHER AUSTRALIAN TERTIARY FOSSIL AREAS OF COMPARABLE AGE

Archer et al. (1989) suggested that Riversleigh System A units may fall 'somewhere between the Ditjimanka and Kutjumarpu and Tarkarooloo LFs of South Australia' a view supported by Woodburne et al. (1993). The latter authors maintained that the base of the mammal-bearing sequence in the Etadunna, Namba and Wipajiri Formations predates that of the Riversleigh succession. They noted in their (lowest) faunal zone A at Lake Palankarinna *Kyeema mahoneyi*, claimed to be the most plesiomorphic potoroid so far found. Formal description of this species has yet to be published and its level of evolutionary development therefore cannot be compared with any of the plesiomorphic Riversleigh potoroids.

Woodburne et al. (1993) also report 2 new species of *Nambaroo* — species A and B, both occurring in faunal zone C from the Ngapakaldi Local Fauna of the Etadunna formation, with species B also present in the Ngama Local Fauna in faunal zone D. Both species are described as more primitive than *Nambaroo saltavus* and *N. tarrinyeri* from the Tarkarooloo Local Fauna, provisionally equated with zone D of the Etadunna Formation at Lake Palankarinna. Archer et al. (1989) correlated Riversleigh System B Local Faunas with the Tarkarooloo and Kutjumarpu Local Faunas. Woodburne et al. (1993) considered the Kutjumarpu Local Fauna of the Wipajiri Formation to represent the uppermost faunal unit in the eastern Lake Eyre Basin, and indicated a possible latest Oligocene age for this Local Fauna. M_1 morphology in *Nambaroo* sp.8 from White Hunter Site is more plesiomorphic than that of any of the *Nambaroo* species in the Tarkarooloo Local Fauna. It retains a hypoconulid, has a straight or only slightly curved paracristid, a short, low anterior cingulid, an under-developed precingulid and a diagonal posthypocristid on the posterior face of the hypolophid. Using the level of evolutionary development argument of Woodburne et al. (1993), the White Hunter assemblage would be older than either the Lake Tarkarooloo or Kutjumarpu Local Faunas, possibly of equivalent age to their zone B+C, estimated by them to be between 25.5-25.0myo. If White Hunter Site is a member of System B, System A sites at Riversleigh would therefore be older, possibly equivalent in age to zone A of the Etadunna formation, i.e., > 25.5myo.

Woodburne et al. (1993) reported a new genus and species of macropodid (their macropodine Gen. *P* sp. A.) from zone C of the Etadunna Formation.

This species was described as more apomorphic in M_1 trigonid morphology than species of *Nambaroo*, having a 'reduced protostylid'. It was considered by them to be potentially ancestral to two new species of *Balbaroo* from the Kutjumarpu Local Fauna. Given this information the new genus must be a balbarine comparable to *Wururoo* (Cooke, this volume) from System B. The comparable levels of development of these genera provide further evidence for equating System B sites with zone B+C of the Etadunna formation. The overall high diversity of balbarine species reported from the various zones of the Etadunna Formation and from the Kutjumarpu Local Fauna (5 species of *Nambaroo*, 2 of *Balbaroo*, 3 of the balbarine genus P, and a species of a macropodine [possibly balbarine?] genus W) is, as has been noted above, typical of the high balbarine diversity of System B at Riversleigh and lends further support to a late Oligocene age for Riversleigh System B, its basal

units being probably equivalent in age to the Ditjimanka and Ngapakaldi Local Faunas of the Etadunna Formation.

At the opposite end of the time scale, derived, lophodont bulungamayines such as gen.*Wan.*, occurring in Riversleigh System C and possibly younger sites, have been suggested elsewhere (Cooke, this volume) to be likely antecedents of plesiomorphic macropodids such as *Hadronomas puckridgi* from the late Miocene Alcoota Local Fauna. Youngest Miocene sites at Riverleigh are therefore probably older than the Alcoota Local Fauna. *Balbaroo* sp.4 has lower molar morphology that is more derived than that of *B. camfieldensis* from the late middle Miocene Bullock Creek Local Fauna. B. sp.4 occurs in the highest levels of System C which may therefore approximate the age of the Bullock Creek Local Fauna.

Kangaroo fossils so far recovered from Riversleigh thus support an age span for pre-Pliocene deposits extending from late Oligocene to at least late middle Miocene. For some Riversleigh sites, e.g., Dunsinane and Cleft of Ages Sites, they suggest ages older than those previously indicated by Archer et al. (1994).

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LITERATURE CITED

ARCHER, M. 1979. *Wabularoo naughtoni* gen. et sp. nov., an enigmatic kangaroo (Marsupialia) from the middle Tertiary Carl Creek Limestone of northwestern Queensland. Results of the Ray E. Lemley Expeditions, part 4. Memoirs of the Queensland Museum 19: 299-307.

ARCHER, M. & FLANNERY, T.F. 1985. Revision of the extinct gigantic rat kangaroos (Potoroidae: Marsupialia), with a description of a new Miocene genus and species and a new Pleistocene species of Propleopus. Journal of Paleontology 59: 1131-1149.

ARCHER, M., GODTHELP, H., HAND, S.J. & MEGIRIAN, D. 1989 Fossil mammals of

Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. Australian Zoologist 25(2): 29-65.

ARCHER, M., HAND, S.J & GODTHELP, H. 1991 Riversleigh. (Reed: Sydney).

ARCHER, M., et al., 1994. List of the principal Riversleigh local faunas and their interpreted relative ages. Abstracts: The Riversleigh Symposium 1994 (Supplement): 28-31.

ARCHER, M., HAND, S.J & GODTHELP, H. 1995. Tertiary environmental and biotic change in Australia. Pp. 77-90. In Vreba, E.S., Denton,G.H., Partridge, T.C. & Buckle, L.H. (eds), Palaeoclimate and evolution, with emphasis on human origins. (Yale University Press: New Haven).

ARENA, R. 1997. The palaeontology and geology of Dunsinane Site, Riversleigh. Memoirs of the Queensland Museum 41: 171-179.

COOKE, B.N. 1992. Primitive macropodids from Riversleigh, northwestern Queensland. Alcheringa 16: 201-217.

1997. New Miocene bulungamayine kangaroos (Marsupialia, Potoroidae) from Riversleigh, northwestern Queensland. Memoirs of the Queensland Museum 41: 269-280.

1997. Two new balbarine kangaroos and lower molar evolution within the subfamily. Memoirs of the Queensland Museum 41: 281-294.

CREASER, P. 1997. Oligo-Miocene sediments of Riversleigh: the potential significance of topography. Memoirs of the Queensland Museum 41: 303-314.

FLANNERY, T.F. 1989. Phylogeny of the Macropodoidea: a study in convergence. Pp 1-46. In Grigg, G. Jarman, P & Hume, I, (eds), Kangaroos, wallabies and rat-kangaroos. (Surrey Beatty & Sons: Sydney).

FLANNERY, T. & ARCHER, M. 1987a. *Hypsiprimnodon bartholomaii* (Potoroidae: Marsupialia), a new species from the Miocene Dwarnamor Local Fauna and a reassessment of the phylogenetic position of *H. moschatus*. Pp 749-758. In Archer, M. (ed.), Possums and opossums: studies in evolution. (Surrey Beatty & Sons: Sydney).

1987b. *Bettongia moyesi*, a new and plesiomorphic kangaroo (Marsupialia: Potoroidae) from Miocene sediments of northwestern Queensland. Pp 759-767. In Archer, M. (ed.), Possums and opossums: studies in evolution. (Surrey Beatty & Sons: Sydney).

FLANNERY, T.F. & RICH, T.H.V. 1986. Macropodoids from the middle Miocene Namba Formation, South Australia, and the homology of some dental structures in kangaroos. Journal of Paleontology 60(2): 418-447.

FLANNERY, T.F., ARCHER, M. & PLANE, M. 1982. Middle Miocene kangaroos (Macropodoidea: Marsupialia) from three localities in northern Australia, with a description of two new subfamilies.

Bureau of Mineral Resources Journal of Australian Geology and Geophysics 7: 287-302.

FRAKES, L.A., McGOWRAN, B. & BOWLER, J.M., 1987. Evolution of Australian environments. Pp. 1-16. In Dyne, G.R. & Bolton, D.W. (eds), Fauna of Australia. Vol.1A: general Articles. (Australian Government Publishing Service: Canberra).

McGOWRAN, B., & LI, Q., 1994. The Miocene oscillation in southern Australia. Rec. S. Aust. Mus. 27(2): 197-212.

MEGIRIAN, D. 1992. Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. The Beagle. 9: 219-248.

    1994. Why the "Systems" terminology used at Riversleigh should be abandoned. Abstracts: The Riversleigh Symposium, 1994: 17.

MYERS, T.J. & ARCHER, M. 1997. *Kuterintja ngama* (Marsupialia, Ilariidae): a revised and extended systematic analysis based on material from the late Oligocene of Riversleigh, northwestern Queensland. Memoirs of the Queensland Museum 41: 379-392.

WOODBURNE, M.O. 1967. The Alcoota Fauna central Australia: an integrated palaeontological and geological study. Bureau of Mineral Resources, Geology and Geophysics Bulletin 87.

WOODBURNE, M.O., MACFADDEN, B.J., CASE, J.A., SPRINGER, M.S., PLEDGE, N., POWER, J.D., WOODBURNE, J.M. & SPRINGER, K.B. 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (late Oligocene) of South Australia. Journal of Vertebrate Paleontology 14:483-515.